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CHROMOSOME MORPHOLOGY IN MAIZE AND ITS RELATIVES

ALBERT E. LONGLEY[1]

INTRODUCTION

Morphological studies on the chromosomes of corn and its relatives have just gone through a second decade of activity. During this period morphological analyses have passed from a consideration of the characteristics of the standard chromosomes to a consideration of chromosomes altered in their morphological features by inversions, deletions, duplications and translocations. This new interest was foreshadowed in several early papers, and now the study of modified chromosomes is in an active phase. This activity became possible by increased quantities of material made available by several groups of corn investigators.

THE STANDARD CHROMOSOMES

Mangelsdorf and Cameron (20) determined the number of chromosome knobs in 162 varieties of corn from western Guatemala and discovered three knobs not previously reported, two on the long arm of chromosome 10 and one terminating the short arm of chromosome 1. These additions to the knobs previously known were incidental to their determination that the corns of this area average 7.9 knobs per plant.

More recently Reeves (43) surveyed the corns from 13 areas south of the United States–Mexican border and found that the average number of chromosome knobs per plant is highest in Guatemala and Mexico, lowest in the central Andean regions.

The surveys of the number of chromosome knobs in corns of the United States by Carter (9) who analyzed the data of the writer

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with refinements; by Brown (3) who studied the knobs in southern dent, northern flint and intermediate dent corns; and by Vachhani (52) who studied the knob number of 20 inbred lines of diverse origin, combined with those of Mangelsdorf, Cameron and Reeves, complete a picture of the distribution of knobs for the corn of the Western Hemisphere.

The combined data from these five studies make it possible to draw certain conclusions regarding the number of chromosome knobs prevalent in corns of certain areas. Corns of Guatemala and Mexico have the highest number of knobs per plant. The corns of commerce usually have five knobs per plant in all areas. The corns with the lowest number of knobs are found in fringe areas. A fringe area may be one far removed from Central America, such as areas where the northern flints grow, or it may be the higher altitudes of Central America, or it may be the Andean region which combines distance from the central region with altitude.

The theory that *Tripsacum* germ plasm has contributed to give certain morphological features prevalent in some corns has stimulated research in the relationship between corn and its wild relatives. Randolph and Hernandez Xolocotzi (42) have confirmed earlier data which showed that the prevalent tripsacums of Mexico are tetraploid and have considerable multiple association of chromosomes initiating microsporogenesis. Their search in Mexico was rewarded also by the discovery of two diploid species, *T. maizar* E. Hernandez X. and *T. zopilotense* E. Hernandez X., which are very different in appearance and when crossed may show interesting combinations of their distinctive characteristics (53).

The chromosomes of another interesting tripsacum have been recently studied, and Brown (3) refers to this species, *T. australe* Cutler and Anderson, as having a low knob number. It seems of interest that the three genera *Tripsacum, Euchlaena* and *Zea* each have a representative or representatives with low knob numbers and that the areas in which *T. australe* and *E. perennis* Hitchc. were found suggest that their low knob numbers are associated with the fringe areas in which they grow.

O'Mara (38) has compared the pachytene configurations of three *Euchlaena* varieties—Florida, Moyuta and Nojoya—in crosses with each other and with maize. Florida and Moyuta in crosses with Nojoya and Maize show abnormal pachytenes due to failure of cer-

tain chromosomes to pair normally. On the other hand, Nojoya–Maize hybrids have normal chromosome pairing, and crossover frequency in the short arm of chromosome 9 is normal. These comparisons indicate that Nojoya teosinte from northern Guatemala is in an intermediate position between the teosintes from southern Guatemala and maize.

Cameron (8) has found that the *2n* chromosome number for *Polytoca macrophylla* Benth. is 40 and that it has no chromosome knobs. Thus the morphological features of the chromosomes of another species from the Orient is available for comparison with its relatives in the new world.

ANCESTRY OF OUR CULTIVATED CORNS

The number of chromosome knobs has played an important role in the interpretation of Mangelsdorf and Cameron (20) and of Reeves (43) that the primary center of origin of our cultivated corns is the central Andean region. They suggest that corn migrated north into Central America from this center and that a secondary center of origin was established in Guatemala.

The presence of corn with low knob numbers in Guatemala suggests to some the possibility that western Guatemala is the primary center of origin of our cultivated corns and that migration north and south was from this center. The Andean region would then be classified as a secondary center of origin at the fringe of the corn-growing belt.

Brown (3) cautions against the use of knobs as indicators of *Tripsacum* germ plasm in corn. He concludes that " Knobs may represent one of the better indicators of relationships in corn " but " more data are needed before one can safely use knob numbers as an index to the amount of *Tripsacum* germ plasm in *Zea*". The real need in all studies of the relationship between corn and its wild relatives is irrefutable morphological and archeological data. From such data it might be possible to establish the place of origin of corn and to clarify the relationship between corn and its wild relatives.

RECIPROCAL TRANSLOCATIONS

Morphologically a translocation represents a new alignment of chromatin in two chromosomes or in two pairs of chromosomes.

Pollen sterility is a very useful indicator of the presence of a translocation, but, as Clark (10) has shown, the fertility of the gametes is frequently altered without visible alteration in the chromosomes. Pollen sterility caused by a translocation is usually at the 50 per cent level, and this sterility is transmitted. Genetically, sterility serves to mark the exchange points of the altered chromosomes, as would a dominant gene at the same location. Since the position of these exchange points can be determined by cytological examination, they become physical points on the chromosomes, and the relative position of other genes to exchange points can be determined.

The aim of cytological analyses of a translocation is to determine the position of the exchange points on the arms of the two altered chromosomes as accurately as possible. Most analyses are made from heterozygous translocations which at pachytene show the crossing of the modified chromosomes at the points of exchange. A few translocations have varying amounts of non-homologous pairing adjacent to the exchange points, making it difficult to determine their positions accurately.

Use of homozygous translocations for determining the exchange points is restricted to translocations in which the break points in the two chromosomes are in regions that have a detectable difference in staining density. When an exchange point is marked by a distinct change in chromosome density, it may be assigned a definite position with considerable accuracy.

It is essential to have good pachytenes for satisfactory translocation analyses. Randolph (40) has shown that certain inbred lines have superior pachytene configurations. Unfortunately the inheritance of this characteristic seems to be controlled by more than one gene. Although the inheritance of good pachytenes is complicated, it is advisable to make every effort to use the better lines for any project involving chromosome analysis.

A few translocations have appeared in genetic stocks, but most of them are the product of radiation treatments of seed or pollen. Anderson (1) and Randolph et al. (41) report the number of translocations isolated from different radiation treatments. It is apparent that translocations soon will be available that combine parts of any two chromosome arms in one chromosome.

Roberts (46) used 13 reciprocal translocations to confirm the

generally accepted idea that translocations do not produce appreciable changes from the normal phenotypes. This fact helps to make translocations useful tools in many fields of corn investigation.

One of the first uses of translocations was to determine the position of genes relative to a fixed point on a chromosome. Anderson and Randolph (2) combined genetic and cytological data from translocations to make linkage maps which include the centromeres for the ten chromosomes of corn. Another use for translocations is the retention through several generations of a gene or genes closely linked to an exchange point. This is possible by retaining the pollen sterility. Such a procedure is being tested in several breeding projects in an effort to retain a desirable character while it is being transferred to an inbred line; e.g., Miller's (36) use of translocations for investigating the inheritance of oil in the corn kernel.

Meiotic segregation of the chromosomes involved in heterozygous translocations may follow the general rule, disjunction of homologous centromeres and the inclusion of one of each pair of homologues in each of the two daughter nuclei. It is possible to visualize a condition in which both altered chromosomes always go to one nucleus and both normal chromosomes to the other nucleus, and no sterile gametes would be produced. Frolik and Burnham (14) looked for such a directed segregation in 50 ring-of-six translocations but failed to find any indication that daughter nuclei with balanced chromosome complements were above or below the number expected from random distribution.

Burnham (4–7) has done much to clarify translocation problems, and discovered that ring-forming translocations have a certain amount of non-disjunction of homologous centromeres when the interstitial segment (distance from the centromere to the exchange point) is too short for frequent crossovers. This unorthodox segregation produces only sterile gametes, but, strangely enough, the pollen sterility in the plant containing the translocation under investigation remains at approximately 50%. He concludes from these observations that the amount of segregation giving fertile gametes is constant and that segregation following non-disjunction and disjunction giving sterile pollen, when combined, makes up the 50% sterile gametes. The amount of non-disjunction of homologous centromeres is greatest when the interstitial segments are

short and crossovers are absent or much reduced. The amount of non-disjunction decreases as the length of the interstitial segment increases.

In contrast to the segregation of ring-forming translocations with short interstitial segments, Burnham (6) finds that chain-forming translocations have little or no non-disjunction of homologous centromeres.

Since non-disjunction of homologous centromeres does not affect the per cent of viable gametes, translocations continue to be useful in measuring linkages between the exchange points and other genes on the modified chromosomes. Certain exceptional translocations are troublesome if used for linkage studies. Occasionally the exchange point is so near the end of one or both of the altered chromosomes that the duplicate-deficient gametes are not always lethal and are transmitted through the egg and infrequently through the pollen. The linkage values are distorted by these extra gametes.

The writer has had the opportunity to analyze a considerable number of translocations. The results of these analyses have been released recently in a mimeographed report by the Naval Medical Research Section (19). In this report it is concluded that various radiation treatments of corn seeds produce transmissible translocations from breaks in the initial chromosomes that were not distributed at random among the ten chromosomes, the 20 chromosome arms or the different sections of the chromosome arms. This non-random distribution is attributed to differences in density. Breaks that reunite to form translocations occur with the highest frequency in the more densely staining ten microns adjacent to the centromeres, and there is an appreciable decrease in the frequency of breaks in the median and distal sections of the chromosome arms. The data suggest, also, that there is a tendency for breaks the same distance from the centromere to be associated more frequently than would be expected on a random basis.

TRISOMICS

Trisomics have played an important role in assigning definite linkage groups to each of the morphologically recognizable chromosomes. Recently Einset (12) found that transmission of trisomics is reduced because of elimination. This elimination during megasporogenesis is greater for short than for long chromosomes. Ibra-

him (15) observed two trisomics in his study of translocation 5–6a. These trisomics 5^6 and 6^5 represent the beginning of a new series of trisomics with modified chromosomes.

INVERSIONS

Inversions, like translocations, require clear well-spread pachytenes for satisfactory analysis. Non-homologous pairing is likely to occur when an inversion is short, and consequently short inversions may be overlooked. It is likely that occasionally pachytenes are classified as normal when in reality short inversions are present.

Morgan (37) used pollen sterility due to chromosome duplication and deficiencies to measure the minimum genetic length of inversions. Some modified chromosomes which cause gametic sterility are the product of breaks–fusions–bridges at meioses. His calculations show the number of crossover units in a known section of a chromosome. For greater accuracy it is suggested that an additional correction be made for the sterility of the parent plant. Such a correction increases his minimum genetic lengths slightly.

Inversions once incorporated in a stock may persist unchanged if the gametes with duplications and deficiencies are not transmitted. An inversion in the short arm of chromosome 8 is an example of an inversion that has persisted and is widely distributed through many genetic stocks.

BREAK–FUSION–BRIDGE AND BREAK–FUSION CYCLES

The earliest illustrations of the break–fusion–bridge cycle were found in paracentric inversions whenever there was a crossover in the inverted region. During the last ten years, McClintock (21–35) has made the break–fusion–bridge cycle a major field of investigation, and her contributions deserve careful consideration. In fairness to Dr. McClintock, it must be pointed out that the material used as a basis for the following discussions is largely from her annual reports, and the data to support her more recent work have not yet appeared.

McClintock's studies began with two types of break–fusion–bridge cycles. She was able to induce the first type, which is the same as that observed in inversions, by using inverted duplications and newly introduced terminal deletions with unsaturated ends.

Regardless of how this type is initiated, it has the following characteristics: Breaks at meiotic anaphase produce terminal deletions and unsaturated ends. Following meiosis there is a chromatid break–fusion–bridge cycle that persists through the subsequent gametophytic divisions and through the life of the developing endosperm. Broken ends usually heal in the zygote cell after fertilization, and the modified chromosome becomes stable and is transmitted from cell to cell in the developing tissue of the plant.

The breakage and relocation of chromosome parts in the endosperms studied by Jones (16, 17) suggest that a similar break–fusion–bridge cycle was active in his material. Such a cycle was demonstrated cytologically by Clark and Copeland (11) who studied the division figures in developing endosperms of material showing a high rate of mosaic formation.

The second type of the break–fusion–bridge complex is illustrated in McClintock's studies of ring chromosomes. She used chromosome 5 with an internal deletion and the complementary ring chromosome. In contrast to the first type, the ring chromosome behaves erratically through the somatic life of the plant. Occasionally at mitosis, instead of two sister rings there is a double dicentric ring or two interlocked rings that fail to move to the poles until broken by the formation of the cell wall. Thus the ring is broken at two places, and, since the breaks may occur at different points, the newly formed rings frequently are unequal in size. The smaller ring may be lost, while the larger ring is usually included in the nucleus of the new cell. Thus this break–fusion–bridge cycle produces islands of tissues with deletions and duplications of the normal chromosome complement.

Recently Fabergé (13) initiated break–fusion–bridge cycles of the first type following ultra-violet radiations. More recently Schultz (50) also reported the effects of ultra-violet radiations on pollen containing a ring chromosome. It is difficult to account for the centromere in the small Dp 3a ring chromosome, since the A locus is thought to be far removed from the centromere of chromosome 3 and the ring represents a short deletion around the A locus. He expected single breaks from the ultra-violet treatments, which would make rods out of rings, but he failed to detect any rods. He found that the higher dosages affected a large percentage of the rings in the endosperm. A similar high frequency of ring losses

was found in the sporophyte. He concludes from the number of rings detected that restitution in the endosperm is lower than in the plant.

A few exceptional plants were observed by McClintock when examining a large number of plants intended for analyzing terminal deletions of the short arm of chromosome 9. These exceptional plants showed variegations which suggested internal rearrangement in this chromosome. It was soon apparent to her that she had found a break–fusion cycle that was active in both the gametophytic and sporophytic life of the plant. Her investigation of the new cycle was aided by the discovery of a dissociation locus, Ds, which when active produces internal alterations in the chromosome, such as deletions, inversions and duplications. A break–fusion in lieu of a break–fusion–bridge cycle is more characteristic of this new cycle, since breaks at slightly different points frequently fuse to give internal alterations instead of the fusions that result in bridges and loss of terminal sections. This break–fusion cycle at the Ds locus is active in both the gametophytic and the sporophytic life of the plant.

McClintock also discovered that the Ds locus is active only if an activation locus Ac is also present in the nucleus. The interactions of the Ac and Ds loci introduces a dosage + time element. An increased dosage of Ac delays the activity of the Ds locus, and when the dosage is sufficiently large the Ds locus may not be active during the developmental life of the endosperm nor the life of the plant. Her recent reports suggest that Ac and Ds are very similar in their effects. A demonstration that the Ac locus is active only when the Ds locus is present will be additional proof of their similarity.

It is difficult to assign a definite physical position for either the Ac or the Ds locus. Ds has been assigned a standard position in the short arm of chromosome 9, and recently the Ac locus has been found near the mid-point of the same arm. Either locus may shift to a new position within a chromosome or to another chromosome at each break–fusion cycle.

A stickiness is thought to characterize both the Ac and the Ds loci. This stickiness initiates breaks and fusions that produce new alignments of chromatin. Such new alignments have been demonstrated both cytologically and genetically.

Alterations in the position of the Ds locus have, in some instances, put it adjacent to a dominant gene. This gene immediately loses its dominant character which returns only when the Ds locus is separated from the gene in subsequent divisions. The effect of the Ds locus on a dominant gene is interpreted as a position effect.

This position effect in corn may be due to the close proximity of a sticky locus to a dominant gene. The sticky locus Ac has recently been shown to be marked by a prominent chromomere which suggests a relationship between heterochromatin and stickiness.

Morphological analysis of chromosomes that have passed through a break–fusion–bridge or a break–fusion cycle presents cytological problems of the most exacting nature. Terminal deletions produced by the first type of break–fusion–bridge cycle are stable after passing through a sporophytic generation. The second type produces alteration in a ring chromosome, causing it to be larger or smaller, but many unaltered rings are retained and are transmitted from generation to generation. The third type which produces many chromosomes with internal alterations, if both the Ac and the Ds loci are present, becomes stable only when the Ac locus is removed from the chromosome complement. This stable chromosome may be maintained unchanged in future generations if the altered chromosome is not lethal to the cell.

Break–fusion–bridge and break–fusion cycles produce modified chromosomes, and frequently these modifications are too minute for cytological detection. Stadler and Roman (51) have found that the alteration A–X3, which they interpret as a deletion of appreciable size including the A locus, could not be detected in the usual cytological preparations. Thus it is not surprising that McClintock has not given cytological data to support all of her studies of altered chromosomes.

THE B-TYPE CHROMOSOME

The B-type chromosome continues to be a fascinating field for study. Randolph (39) found types C, D, E and F of this chromosome that are progressingly smaller. These smaller types are thought to be induced by breakage and loss of the distal portion of the typical B. Like typical B-types these smaller chromosomes

have a transmission through the pollen significantly different from that through the egg.

Roman (47) has shown why there is a difference in egg and pollen transmission of B-type chromosomes. He used a translocation involving an A- and a B-type chromosome and found that, although the mega- and micro-sporogenesis are relatively normal, the B interchange chromosome with the B centromere non-disjoined at the second division of the microspore nuclei because of a malfunctioning of its centromere and produced a deficient and a hyperploid nucleus. Appropriate markers showed that a hyperploid embryo and a deficient endosperm, or a deficient embryo and a hyperploid endosperm, were produced after fertilization.

More recently Roman (48) found that the hyperploid nuclei have an advantage over the deficient nuclei in effecting fertilization of the egg. Non-disjunction of B-type chromosomes at the division of the microspore nucleus and directed fertilization result in transmission of B-centromeres through the pollen quite different from their transmission through the egg. All divisions preceding egg formation were shown to be approximately normal.

Morphologically, translocations involving B-type chromosomes are relatively easy to detect and analyze, due to the characteristic pycnotic distal portion of the B-chromosome. A unique feature of translocations involving an A- and a B-type chromosome is the opportunity they afford to produce plants that are monosomic for the translocated section of the A chromosome. Roman and Ullstrup (49) have clearly demonstrated the use of A-B chromosomes to locate the position of a gene.

ABNORMAL FORM OF CHROMOSOME 10

The abnormal form of chromosome 10 is recognized by the increased length of its long arm resulting from addition of a strongly pycnotic piece of chromatin. The presence of this added piece might be explained by assuming that there had been a translocation of chromosome 10 with some other chromosome, but such an explanation has no support because none of the other chromosomes possesses a section that resembles this added piece.

Two papers by Rhoades (44, 45) drew attention to the peculiar effect of this abnormal chromosome. He found that after mega-

sporogenesis, the abnormal chromosome was present in 70% instead of the expected 50% of the megaspores. He also found that this chromosome caused the appearance at meiotic metaphases and anaphases of secondary centric regions near the end of many chromosome arms.

The writer (18) later showed that the preferential segregation discovered by Rhoades is not restricted to chromosome 10 but affects the segregation of other chromosomes that are heterozygous for knobs. The preferential segregations and the appearance of secondary centric regions due to the presence of the abnormal form of chromosome 10 may prove to be associated phenomena. Both Rhoades and the writer have maintained an interest in this modified chromosome 10, and the present interest in the role of heterochromatin is added stimulus to continue the earlier studies.

SUMMARY

Several publications deal with the distribution of chromosome knobs among the corn varieties of the western hemisphere.

The ancestry of our cultivated varieties of corn is a problem that seems to require more convincing data to fix definitely their place of origin and the relationships between corn and its wild relatives.

Morphological studies of corn chromosomes have entered a new phase, with the analyses of chromosomes modified by translocations, inversions, deletions and duplications.

Altered chromosomes are serving as tools to aid in locating genes more accurately, to attack the problems of gene interaction, and to scrutinize the dominant–recessive character of the gene.

It has been found that a piece of chromatin foreign to the normal chromosome set, when added to the long arm of chromosome 10, results in the formation of secondary centric regions in other chromosomes and preferential segregation at megasporogenesis of all chromosomes heterozygous for knobs.

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SOUTHERN SWAMPS AND MARSHES[1]

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INTRODUCTION

The area under consideration in this review includes all the States from Virginia to Florida and west to eastern Texas and eastern Oklahoma. On its northern extremities it comprises portions of southeastern Missouri, southern Illinois and southwestern Kentucky. The area coincides almost exactly with the red and yellow soil groups of the United States (Marbut, 1935). Physiographically it comprises most of the Atlantic and Gulf coastal plains and nearly all of the Mississippi alluvial plain. It includes most of the Piedmont and Ouachita provinces and the southern portions of several other provinces.

Most southern swamps and marshes are located in the coastal plain or in the Mississippi alluvial plain. The older terraces of the coastal plain have been eroded into an uneven topography with enough relief to drain the uplands, but the lower ones are in a flat condition of low relief with relatively poor drainage. There is considerable variation, however, in soil texture, a basic factor of considerable importance in the local distribution of hydric plants. The rolling sandy uplands are too dry for hydric communities, the flat

[1] Suggestions by Dr. E. O. Hughes, Dr. E. L. Rice and Dr. L. M. Rohrbaugh in the preparation of this article are herewith gratefully acknowledged.

uplands are seasonally excessively dry or very wet with the result that bays, pocosins, shrub bogs and grass-sedge bogs are the rule (Wells, 1942). In the alluvial plains the ridges are clothed with hardwood forest, but the flats and sloughs are occupied by swamps or marshes.

RELATION TO SEA LEVEL

It is generally accepted that the Atlantic coast is gradually subsiding. Marmer (1948) reported that a continuous rise of 0.02 foot per year in sea level occurred from 1930 to 1948: "To say that sea level has risen with respect to a fixed point on shore is only another way of saying that the fixed point has subsided with respect to sea level. It is not at all improbable that both may have occurred—some actual subsidence of the coast and some actual rise of sea level".

Mangrove peat beds much thicker than the tidal range have been found in Florida. A ten-foot deposit of peat in a region with a tidal range of three feet is held to indicate a rise in sea level of about seven feet (Davis, 1940). Many evidences of subsidence have been given for the Gulf coastal plain (Russell, 1936): delta flank depressions, disappearance of coastal islands, abandonment of inhabited islands due to increasing wetness and salinity, red-yellow soils under marsh deposits, sinking of Indian mounds, and the sinking and near disappearance of the Eads jetties at the mouth of the Mississippi River. Geologists believe that the islands off the coast of Mississippi were at one time a part of the mainland and that the entire Gulf coast is slowly sinking (McGee, 1891). Soil samples taken at different places on Horn Island and from the bottom of Mississippi Sound, similar to those on the mainland, appear to support this hypothesis (Pessin et al., 1941). Remains of upright stumps in the marshes of southeastern Louisiana are also believed to indicate subsidence (Brown, 1936). Apparently the evidence is overwhelming in favor of subsidence for both the Atlantic and Gulf coasts. This subsidence of relatively flat lands near sea level has contributed greatly to the formation of extensive areas of swamps and marshes. Indeed it would be difficult to explain the presence of such extensive wetland areas along the coastline of the southern United States on any other basis.

TERMINOLOGY

A swamp is a woody community occurring in an area where the soil is usually saturated or covered with surface water for one or more months of the growing season. This concept of swamps has been held by most of the workers on southern swamps. Davis (1943) would eliminate frutescent communities from this category, although the red mangrove, black mangrove, buttonwood and buckbrush–marsh elder communities he described are essentially frutescent in nature. In the present paper, swamps with shrubby dominants include swamp privet–water elm, buttonball, dogwood, willow, alder–birch, buckbrush–marsh elder and shrub bog communities. The peat-forming swamps have often been referred to as "bogs" (Buell, 1939; Wells, 1928, 1942, 1946). These peaty swamps comprise bays, white cedar bogs, pine pocosins and evergreen shrub bogs. Authors who have referred to these communities as "swamps" include Garren (1943), Harper (1926), Kearney (1901) and Shaler (1885). The term "swamp" is used in this paper because of considerable prior usage, since sphagnum moss does not exercise a selective influence on the community, and because there are many intergradations between other swamps and the peaty swamps.

A marsh is a grass–sedge–rush community occurring in an area where the soil is usually saturated or covered with surface water for one or more months of the growing season. The sea coast marshes are subject to tidal inundation periodically. Daily tides usually inundate the marsh proper, but only the flood or storm tides cover the zonal or transitional (salt grass and reed–cane) communities. Other transitional communities designated herein as "shallow marshes" include low marshes, wet prairies, wet meadows, savannahs and wet pine barrens of other investigators (Davis, 1943; Garren, 1943; Hotchkiss et al., 1947; Kearney, 1901; Wells, 1928, 1942; Wright et al., 1932). The term "marsh" ordinarily does not include submerged, floating or emergent stages of shallow lakes and ponds. In some cases where a floating mat (flotant) is composed mainly of grasses and sedges, and can be traversed readily on foot, a true marsh is approximated. Some emergent stages, of proper composition, may be designated as "marshes".

LIST OF MAJOR TYPES OF SWAMPS AND MARSHES

Fresh Water Swamps

Deep Swamps

DEFINITION. Deep swamps are fresh water, woody communities, with surface water throughout most or all of the growing season.

COMMUNITIES

*Southern cypress–tupelo gum (*Taxodium distichum–Nyssa aquatica*).

Swamp gum–pond cypress (*Nyssa biflora–Taxodium ascendens*).

CHARACTERISTICS. Relatively tall, deciduous trees, with swollen bases and "knees", and abundant epiphytes. Frutescent and herbaceous species few or none.

Shallow Swamps (transitional communities)

DEFINITION. Shallow swamps are fresh water, woody communities, the soil of which is inundated for only short periods during the growing season.

COMMUNITIES

Black willow–sandbar willow (*Salix nigra–Salix interior*).

Buttonball–dogwood–willow (*Cephalanthus–Svida–Salix*).

Overcup oak–water hickory (*Quercus lyrata–Hicoria aquatica*).

Hackberry–elm–ash (*Celtis–Ulmus–Fraxinus*).

Maple–red gum–oak (*Rufacer–Liquidambar–Quercus*).

Alder–birch (*Alnus–Betula*).

CHARACTERISTICS. Deciduous trees or shrubs without evident hydrophytic characters except for production of water roots in buttonball and willows and swollen bases in green ash.

Peaty Swamps

DEFINITION. Peaty swamps are oxylic, peat-forming, sclerophyllous woody communities, with surface water only during a part of the growing season.

COMMUNITIES

Red bay–sweet bay (*Tamala pubescens–Magnolia virginiana*).

Pond pine–slash pine (*Pinus serotina–Pinus caribaea*).

Southern white cedar (*Chamaecyparis thyoides*).

Evergreen shrub swamp (*Ilex–Cyrilla–Zenobia*).

* Plant names according to Small (1933).

CHARACTERISTICS. Sclerophyllous, evergreen trees or shrubs, including many ericaceous species. Frutescent and herbaceous plants numerous.

Salt Water Swamps

DEFINITION. Woody plant communities in brackish or saline habitats.

COMMUNITIES

Mangrove swamps (usually with surface water)
Red mangrove (*Rhizophora Mangle*).
Black mangrove (*Avicennia nitida*).
Transitional communities (usually without surface water)
Buttonwood (*Conocarpus erecta*).
Buckbrush–marsh elder (*Baccharis–Iva*).

CHARACTERISTICS. Mangrove swamps are characterized by evergreen trees, with pneumatophores and partial vivipary. Transitional woody communities exhibit no visible hydrophytic characters.

Fresh Water Marshes

Deep Marshes

DEFINITION. Deep marshes are fresh-water grass–sedge–rush communities the soil of which is covered by water throughout most or all of the growing season.

COMMUNITIES

Giant cut grass (*Zizaniopsis miliacea*).
Cattail–bulrush–maiden cane (*Typha–Scirpus–Panicum*).
Saw-grass (*Mariscus jamaicensis*).

Shallow Marshes (wet meadows)

DEFINITION. Shallow marshes are fresh-water, grass–sedge–rush communities, in which surface water is usually present for only a small part of the growing season.

COMMUNITIES

Panic grass–horned rush (*Panicum–Rynchospora*).

Salt Marshes

DEFINITION. Grass–sedge–rush communities in brackish or saline habitats.

COMMUNITIES (in order of decreasing water depth)

True marshes (with surface water most of the time)
Salt cane (*Spartina alterniflora*).
Couch grass–salt grass–black rush (*Spartina–Distichlis–Juncus*).

Marsh grass–dropseed (*Spartina–Sporobolus*).
Zonal communities (with little or no surface water)
Salt grass (*Distichlis spicata*).
Reed–cane (*Phragmites–Spartina*).

DEEP FRESH-WATER SWAMPS

Extensive southern cypress–tupelo gum swamps (*Taxodium distichum–Nyssa aquatica*) occur in the floodplains of large rivers, especially of the Mississippi River drainage. The black gum–pond cypress (*Nyssa biflora–Taxodium ascendens*) swamps are much more common on the uplands of the coastal plain and are rarely encountered in the floodplains of large rivers. These forests correspond to cover types 92, 93, 94 and 95 of the Committee on Forest Types of the Society of American Foresters (Hawley et al., 1940). Either southern cypress or tupelo gum may occur in pure stand (Mattoon, 1915), but pure tupelo gum stands are often due to clear cutting of cypress–tupelo gum stands (Putnam, 1951). One of the most interesting stands of southern cypress is a pygmy cypress swamp growing on thin soil overlying a limestone reef in the Everglades of Florida. The trees appear to be whitewashed and are typically only six to eight feet tall, although they may be taller where the soil is deeper (Small, 1933). Scrubby cypress are also found scattered throughout the Everglades. These may be spaced evenly or may occur in the form of domes (from the contour of the group) dispersed throughout the marsh (Davis, 1943). Fragmentary pure stands of cypress are found in southeastern Oklahoma (Bruner, 1931).

Southern cypress and tupelo gum are found mixed together in the flood plains of large rivers or mixed with swamp black gum and pond cypress in the coastal plain (Mattoon, 1915). Along the edges and in the shallower parts of coastal plain swamps, *Tamala pubescens, Magnolia virginiana, Pinus caribaea, Pinus serotina* and *Chamaecyparis thyoides* are common associates (Beaven et al., 1939; Gano, 1917; Kearney, 1901; Mattoon, 1915). In general, the average water depth is somewhat greater in the floodplain swamps than in those of the uplands. All deep swamps are alike in that the water level drops periodically below the soil surface during exceptionally dry summers (Mattoon, 1915; Wells, 1942). It is maintained by some (Hawley et al., 1940) that tupelo gum

" frequently occupies deeper swamps or sloughs than the southern cypress ". This may possibly be true, but the tupelo gum is much less tolerant of flooding than is the southern cypress (Penfound, 1949).

All dominants of deep swamps produce so-called pneumatophores. Both cypresses produce conical pneumatophores, the swamp black gum possesses arching roots which often approximate the conical form, and the tupelo gum produces massive rounded " knees " which arise in the same manner as those of the swamp black gum (Kearney, 1901; Wells, 1942).

In 1942 Wells stated that the cypress " knees " were structures involved in respiratory gas exchange. In this connection it should be pointed out that cypress does not produce " knees " on unflooded lands or on soils inundated with water continuously but only on land which is subject to alternate flooding and draining. Cypress " knees " are absent, therefore, where presumably most needed—in deep water. The wood of cypress " knees " is not aerenchymous and has a specific gravity about the same as that of the wood of the trunk. In view of these facts it is doubtful that cypress " knees " are of any great value in respiratory exchange. Regarding the question of anchorage, quotation from Mattoon's work (1915) seems justified: "At its lower end the knee has a downward-reaching, pronged root system, smaller but similar in appearance to the main root system beneath the tree. The knee might be termed a secondary sort of tree . . . . The mass of interwoven horizontal roots, with the aid of hundreds of vertical roots beneath the knees, binds the associated soil material, and furnishes a stable support for the weight of the tree ". It will be observed from photos in one publication (Brown, 1943) that these roots may be produced in the absence of cypress " knees ". It should be noted that cypress grown on dry land and in deep water, and without knees, are also very resistant to wind-throw. From the evidence to date one can conclude only that the function of cypress " knees " is not known.

All four major components of cypress–gum swamps produce buttresses or swollen bases. The height of these swollen bases depends on the height of water level in the early part of the growing season. Buttress-development, as well as the production and height of " knees ", is considered as a response to aerated water

(Kurz et al., 1934). Hanging bell-shaped structures on cypresses in deep water in Reelfoot Lake were explained on the same basis, since the water below the "bell" would possess little oxygen (Kurz et al., 1934). Football-shaped hanging swellings were formed on both tupelo gum and bald cypress at the new pool level in Lake Chicot, Louisiana, four years after impoundment (Penfound, 1949). The greatest swelling occurred at the new pool level and extended gradually from this point up and down the trunk. It is probable that the greatest swelling occurs at the point where aerated water is present for the longest period but that the trunk diameter decreases gradually to the normal trunk, even above the highest water level.

The seeds of all woody fresh-water swamp species require dewatering or strandage if germination is to be accomplished (Hall et al., 1946). For seedlings of the southern cypress to become established "the seed must sprout when not submerged, and the seedlings must grow to sufficient height during the first year to stay above the floods except for a few days during the second year" (Demaree, 1932). For this reason the southern cypress is rarely found in water bodies having an average seasonal fluctuation of more than ten or twelve feet. Cypress seeds have, however, germinated while floating on water (Welch, 1931). Welch found also that seedlings which were completely submerged for 42 days produced new shoots when the tips were exposed to the air again. It is, therefore, quite possible that some other factor than oxygen may be critical in seed germination of the southern cypress. Seeds of the water hyacinth were observed not to germinate under water under natural conditions (Penfound et al., 1948), but when the temperature of the water was raised, abundant germination was obtained (Hitchcock et al., 1949). Further examination on the above problems is needed before final conclusions can be reached.

SHALLOW FRESH-WATER SWAMPS

Shallow swamps are woody communities developed on saturated soils or on soils subject to periodic flooding during the growing season. They occur typically as narrow bands along streams or around ponds and lakes. All gradations from deep swamps to mesic forests are represented in the shallow swamp series. The willow swamp (*Salix nigra–Salix interior*) occurs in habitats on

floodplains having the greatest depth of water and the longest hydroperiods of any of the shallow swamps. " Willow thrives in saturated or poorly drained soil from which other hardwoods are excluded " (Oosting, 1942). It includes buttonball (*Cephalanthus occidentalis*), swamp privet (*Forestiera acuminata*), black willow (*Salix nigra*) and sandbar willow (*Salix interior*) as the predominant species, any one of which may occur in pure stand. The buttonball occurs in the deepest water and may be found in many cypress swamps. Swamp privet is often found in pure stands around borrow pits and lakes. Black willow occurs in a variety of habitats but exhibits its best development in fine silt or clay in relatively stagnant water, whereas sandbar willow is found in sandy areas, in lakes and streams.

A shrubby community with a water tolerance similar to that of the willow swamp is the *Cephalanthus–Svida–Salix* associes. This community, composed " of such species as *Cephalanthus occidentalis, Svida Ammomum,* and *Salix longipes,* is especially characteristic of rocky intermittent streams and of gravel flood plains " (Little et al., 1936). With the addition of *Alnus rugosa* and *Itea virginica* this associes occurs just outside the band of *Taxodium distichum* in lakes in southeastern Oklahoma (Little et al., 1931).

The overcup oak–water hickory (*Quercus lyrata–Hicoria aquatica*) associes corresponds to type 89 of the Society of American Foresters (Hawley et al., 1932). It occurs in poorly drained depressions, sloughs and shallow swamps, primarily in Louisiana and Mississippi. Since its principal species, including *Diospyros virginiana* and *Fraxinus pennsylvanica,* " remain dormant and leaf out a month or so later than most species, they endure submergence better " (Putnam, 1951).

The hackberry–elm–ash (*Celtis–Ulmus–Fraxinus*) associes occurs on low flats and sloughs in the Mississippi alluvial plain. It is a temporary type following heavy cutting and fire. The predominant species are *Celtis mississippiensis, Ulmus americana, Fraxinus pennsylvanica, Hicoria aquatica* and *Quercus phellos.* " Occasional small stands of pure ash may occur almost anywhere within the type but most notably on moist flats or in shallow sloughs " (Putnam, 1951). From the above discussion it can be inferred that this forest is a transitional type between a swamp and a mesic forest.

Another transitional swamp type is the *Rufacer–Liquidambar–Quercus* swamp complex. Hotchkiss et al. (1947) called it the transition or river swamp and listed red maple (*Rufacer rubrum*), red gum (*Liquidambar styraciflua*) and pin oak (*Quercus palustris*) as the dominant species. In the lower Mississippi alluvial plain *Quercus Nuttallii* and *Q. phellos* are present in place of *Q. palustris* (Putnam, 1951). The *Rufacer–Liquidambar–Quercus* swamps may vary greatly in composition. Species in order of decreasing water tolerance include *Salix nigra, Populus deltoides, Fraxinus pennsylvanica, Rufacer rubrum, Liquidambar styraciflua, Quercus palustris* and *Platanus occidentalis.* These species may occur in pure stand or in almost any combination.

The *Alnus–Betula* associes occurs primarily in small stream valleys that traverse the Piedmont, coastal plain and other provinces. In Maryland, "alder (*Alnus serrulata*) characterizes sites on ground that is usually covered with a very thin sheet of water (less than one or two inches) . . . . These swamps are ordinarily invaded by River Birch (*Betula nigra*)" (Hotchkiss et al., 1947). They describe also a shrub swamp (seepage-fed) which is characterized by the addition of several oxylic species. At Piedmont, North Carolina, wet poorly drained areas are invaded by alder and willow. "With stability and drainage the dominants are replaced by birch or sycamore which in turn develop an understory of elm, ash, and red maple" (Oosting, 1942). In Oklahoma "the *Betula–Salix* association of *Betula nigra* and *Salix nigra* occasionally is present along silt banks of the larger streams . . ." (Little et al., 1936). From the evidence it appears that alder and willow are more water-tolerant than birch, and that birch constitutes a later successional stage than either alder or willow.

PEATY FRESH-WATER SWAMPS

The peaty swamps (bays, pine pocosins, cedar bogs, evergreen shrub bogs) are found on poorly drained, flat, interstream areas of the lower terraces in the Atlantic and Gulf coastal plains. They are peat-forming woody vegetational units, usually growing in acid soil, in which the surface water usually disappears during summer. These swamps include the following communities: red bay–sweet bay (*Tamala–Magnolia*); pond pine–slash pine (*Pinus serotina–Pinus caribaea*); southern white cedar (*Chamaecyparis thyoides*);

and evergreen shrub swamp (*Ilex–Cyrilla–Zenobia*). Another community related to the above is the shallow marsh (*Panicum–Rynchospora* associes), variously designated as low marsh, sedge meadow, wet meadow or savannah by other investigators.

The *Tamala–Magnolia* associes (red bay–sweet bay swamps) are characterized by a more or less dense growth of evergreen trees, including *Tamala pubescens, Tamala Borbonia, Magnolia virginiana, Gordonia lasianthus, Pinus serotina* and many shrubs (Gano, 1917; Harper, 1926). Most of these species occur on the margins of the deep (black gum) swamps and in the southern white cedar forest of the Dismal Swamp (Kearney, 1901). Many of them also occur in cypress heads and cut-over shallow cypress swamps in the Okefinokee swamp (Wright et al., 1932). Although the bay swamps apparently have not been studied intensively, they are considered climax by some workers, since the southern white cedar swamp reverts to the *Tamala–Magnolia* swamp when protected from fire (Buell et al., 1943). It should be pointed out, however, that none of the hydric communities can be considered climax because none of them is controlled by climate.

The *Pinus serotina–Pinus caribaea* associes (pine swamp, pine bog, pine pocosin) corresponds to forest cover types 74, 91 and 92. *Pinus caribaea* does not occur in the northern part of the range of the community. In the southern portion either pine may occur in pure stand or in mixed stands, often with the addition of pond cypress and swamp black gum (Hawley et al., 1932). "Pure stands of slash pine sometimes result from dry-season fires in the southern white cedar swamp type" (Garren, 1943). In the longleaf–slash pine type, *Pinus caribaea* is confined to those moist sites which escape repeated burning. In the slash pine–pond cypress community in Louisiana, no shrub stratum occurs, but a dense herbaceous stratum, separable into three layers, covers the ground (Penfound et al., 1937). It should be noted that the pond pine communities of North Carolina possess little herbaceous vegetation and are often changed by fire into shrub swamps in which *Pinus serotina* occurs only as scattered relicts among the fire-resistant shrubs (Wells, 1942, 1946).

The *Chamaecyparis thyoides* consocies (southern white cedar swamp) has been studied by many investigators (Ackerman, 1923; Buell et al., 1943; Korstian et al., 1931; Wells, 1942). This com-

munity corresponds to forest cover type 90 which is "confined to sandy-bottomed, usually peaty interior and river swamps, wet depressions and stream banks" (Hawley et al., 1940). The site occupied is composed of peat underlain by sand (Korstian et al., 1931). Apparently it may be found in water as much as two feet deep, but occurs in the Great Dismal Swamp only in areas that are subject to partial desiccation at some period of the year (Shaler, 1885). It often occurs in pure stand but may be intermixed with species of the red bay–sweet bay, pond pine–slash pine and black gum–pond cypress swamps. An open peat soil is required for establishment of the southern white cedar, seedlings often being observed in the rollways and tramways after logging (Ackerman, 1923). Its ecesis is favored by fire when the raw surface peat is too wet to burn (Buell et al., 1943). Once established, the southern white cedar is highly susceptible to fire, severe burning sometimes resulting in pure stands of slash pine or a sprout stand of black gum (Garren, 1943). When protected from fire it "gives way to the bog climax of *Tamala pubescens, Magnolia virginiana,* and *Cyrilla racemiflora*" (Buell et al., 1943). The southern "white cedar forests may be regarded as special fire serclimaxes", the special conditions occurring so infrequently as to limit the occurrence of this interesting community (Wells, 1942).

The *Ilex–Cyrilla–Zenobia* associes (evergreen shrub swamp) has been investigated by Kearney (1901) and notably by Wells (1928, 1942, 1946). It is formed when the trees of the southern white cedar swamp are removed by cutting or fire. It is possible also that the shrub swamp arises from burning in either the *Tamala–Magnolia* or *Nyssa–Taxodium* swamps (Wells, 1946). The community occurs in areas which are flooded with water in early spring but in which the water level falls well below the soil surface in the latter part of the growing season. Upland plants are kept out by the inundated condition in the spring; deep swamp and marsh plants by the desiccated condition in summer and fall (Wells, 1942). The most important dominants are *Ilex glabra, I. lucida, Zenobia cassinefolia, Arundinaria tecta, Magnolia virginiana* and *Cyrilla racemiflora.* The important genera of this associes are as follows: *Clethra, Itea, Xolisma, Leucothoe* (Kearney, 1901); *Ilex, Morella, Cyrilla* (Wells, 1928); *Cyrilla, Zenobia* (Wells, 1946). *Smilax laurifolia,* a vigorous vine, appears to be a universal com-

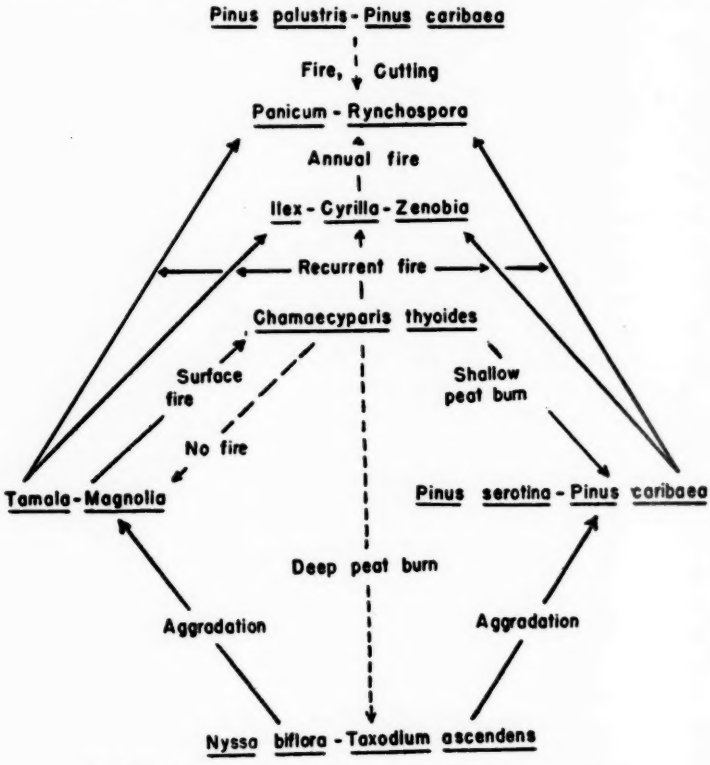
ponent of this community. It should be observed that many of these shrubs and vines are pioneers on the elevations in cypress–gum and other swamps (Buell et al., 1943). In this community recurrent fire is an ever present influence, with new shoot growth being produced by root crowns. " Solution of the problem as to what will happen without fire must remain largely hypothetical, for demonstration areas are practically unknown in the south " (Wells, 1942).

The intimate relation between all the peaty swamps is suggested in the following reports: *Tamala–Magnolia* swamps often include *Pinus serotina* and *Pinus caribaea* (Davis, 1946); the white cedar swamps in Florida often comprise *Tamala pubescens, Magnolia virginiana* and *Pinus caribaea* (Harper, 1926); *Ilex–Cyrilla–Zenobia* swamps usually include *Tamala pubescens, Magnolia virginiana, Pinus serotina* and even *Nyssa biflora* (Wells, 1946). The probable relationships are shown in the accompanying outline. Although the first invaders of deep ponds are dominants of the *Nyssa–Taxodium* associes, it is probable that the dominants of the *Tamala–Magnolia* and *Pinus serotina–Pinus caribaea* swamps more often become established in shallower ponds, since they are commonly marginal to the cypress–gum swamps (Gano, 1917). Formation of peat in the *Tamala–Magnolia* and *Pinus* spp. associes appears to be prerequisite to formation of the *Chamaecyparis thyoides* and *Ilex–Cyrilla–Zenobia* swamps. The *Tamala–Magnolia* swamp is favored by fire protection but is replaced by *Chamaecyparis thyoides* by devastating surface fire (Buell et al., 1943). It reverts to pine swamp with shallow peat burns (Garren, 1943) and may revert to a cypress–gum swamp with deep peat burns. With recurrent fire the red bay–sweet bay, pond pine–slash pine, and white cedar swamps may be converted to the *Ilex–Cyrilla–Zenobia* associes or even may be reduced to the shallow marsh (*Panicum–Rynchospora* associes). It should be noted, however, that the shallow marsh is characterized by a mineral soil (Wells, 1942) and could not arise in a peaty area without aggradation by inorganic sediments.

SALT-WATER SWAMPS

The only halophytic swamp occurring in deep water is that of the red mangrove (*Rhizophora Mangle*). The red mangrove swamp

has been described by many workers, notably Bowman (1917), Davis (1940), Harshberger (1914) and Harper (1927). Young seedlings may become established on mineral soils (sand, marl, shell fragments) below mean low tide levels. " In about 20 or 30 years the young mangroves become so thickly entangled that their



Probable community relations in the peaty swamp complex.

roots act as natural weirs to catch debris " (Davis, 1940). As the soil is built up, *Languncularia racemosa* may become established, and the black mangrove (*Avicennia nitida*) invades from the upper edge. In general, trees of the mature *Rhizophora* consocies are about eight inches in diameter and 30 feet tall, but in some cases they attain a diameter of 26 inches and a height of 100 feet and are of considerable value for timber.

The vivipary in the red mangrove has been the subject of some discussion. Uphof (1941) states that in *Rhizophora* " the conspicuous large taproot hangs from the pendant fruits. After having reached a certain degree of maturity, the young seedlings drop from the mother plant and fall straight into the mud where they then develop lateral roots ". Davis (1940) found that " the hypocotyls are more often curved than straight, and not many of them fall with enough force, or straight enough, to plant themselves on the spot. When they fall into water most of them are shunted off and bob up after the force of the fall is spent, to float away ". They may float for a year or more, and as much as a thousand miles, where many of them strike bottom and effect ecesis.

The black mangrove (*Avicennia nitida*) consocies occurs at the upper edge of the red mangrove swamp where the soil is flooded only irregularly. The community consists of *Avicennia nitida* with few or no companion species by the time the plants attain heights of 15 feet or more. In areas of less dense cover, the predominant companion species are *Batis maritima, Distichlis spicata* and *Spartina alterniflora.* Because of these marsh species, Davis (1940) designates the community as the *Avicennia*–salt marsh associes. In this case it appears that we are dealing with two ecologically equivalent communities and that the black mangrove eliminates the salt marsh species under optimum growth conditions. The black mangrove " trees may be 12 inches in diameter and 40 feet high ". They produce unbranched pneumatophores " which grow upward through as much as a foot of soil and 2 or 3 feet of water " (Davis, 1940). Seeds of the black mangrove fall from the trees, germinate, float about in the water for long periods, and germinate when they are stranded on the soil surface.

The buttonwood (*Conocarpus erecta*) consocies occurs on the landward fringe of the black mangrove consocies where it is rarely or never flooded by sea water. It is " an ecotone or transition zone between mangrove vegetation and some inland, upland, non-halophytic form of vegetation " (Davis, 1940). The buttonwood consocies usually includes *Conocarpus erecta, Avicennia nitida* and *Sabal Palmetto* as the predominant woody species and a host of scattered herbaceous species. It should be mentioned that *Laguncularia racemosa* occurs in the red mangrove, black mangrove and buttonwood zones and may form small stands in any one of these communities (Davis, 1940).

The buckbrush–marsh elder (*Baccharis–Iva*) associes, or *Baccharis–Hibiscus* association of Kearney (1901) is a shrub swamp which occurs naturally on the low ridges of brackish streams and on the shorelines of brackish lakes. It also occurs on spoil banks along salt marsh canals and in drained brackish areas. The predominant species are *Baccharis halimifolia, Iva frutescens, Panicum virgatum* and sometimes *Hibiscus moscheutos. Baccharis halimifolia* and *Panicum virgatum* either disappear or are confined to the higher ridges in areas of high salinity. With reference to water levels, this community occupies about the same position in brackish areas as the *Conocarpus* consocies does in highly saline areas.

MINOR SWAMP TYPES

Water elm (*Planera aquatica*) and swamp privet (*Forestiera acuminata*) often occur in cypress–gum swamps and may form a distinctive swamp type (Brown, 1943; Penfound, 1949). In Catahoula Lake, Louisiana, a lake of wide amplitude of water levels, the water elm–swamp privet community occurs below (in deeper water than) the cypress forest (Brown, 1943). The pop-ash (*Fraxinus caroliniana*) often occurs in pure stand in ponds of southern Florida (Davis, 1943). Green ash (*Fraxinus pennsylvanica*) often occurs in pure stands and exhibits buttressed bases in shallow ponds. Another interesting community in ponds of the coastal plain is that of the mayhaw (*Crataegus aestivalis*) consocies. Although the canebrake (*Arundinaria gigantea* consocies) is not ordinarily considered as a swamp community, it covers considerable areas in the open parts of the Dismal Swamp. Apparently it becomes established after cutting in both the black gum and white cedar swamps, and spreads readily by means of underground stems (Kearney, 1901).

The custard-apple (*Annona glabra*) swamp, now almost extinct, was discussed by Harshberger (1914) Harper (1927) and Davis (1943). The custard-apple swamp was best developed on the south shore of Lake Okeechobee. "This zone was a seasonally flooded swamp or low hammock forest about 3 miles wide made up mainly of a dense growth of the custard-apple . . . that grew in a curiously buttressed, branch form . . . . The custard-apple forest gradually gave way to a thicket swamp zone inland, and this zone

contained mainly the elderberry, *Sambucus Simpsonii* Rehder, and the common willow of south Florida, *Salix amphibia* Small" (Davis, 1943). The buckbrush (*Baccharis halimifolia*) is also common in the elderberry–willow swamp. It should be mentioned here that willows, elderberries and buckbrush are characteristic of cut-over and partially drained deep water swamps.

Palm "savannahs" occur in Georgia and Florida. Perhaps the most remarkable is that on the Indian Prairie, northwest of Lake Okeechobee, Florida. This savannah consists of the cabbage palm, *Sabal palmetto,* together with wetland shrubs, scattered throughout a marsh of *Mariscus jamaicensis and Spartina Bakeri* (Harper, 1927). At the southern tip of Florida there is a relatively flat area, "nearly all subject to inundation by high tides and in the rainy season, but dry enough in winter and spring". This region, known as the coastal prairie, differs from the Everglades in that it is subject to flooding by salt water and includes stunted cypress or mangroves scattered throughout much of the marsh area. These mixtures of swamp and marsh dominants appear from photographs like true savannahs (Figures 50 and 51, Harper, 1927). The *Avicennia*–salt marsh associes is described as a swamp by Davis (1940). Actually it is a swamp invading a marsh but often gives the appearance of a savannah. Usually *Distichlis spicata* is the marsh-dominant, but *Juncus Roemerianus* is the predominant marsh species in the "salty savannah" pictured by Harper (Figure 54, 1927).

DEEP FRESH-WATER MARSHES

Of the deep marshes, the giant cut grass (*Zizaniopsis miliacea*) consocies occurs in the deepest water and has the longest hydroperiod. Little et al. (1936) report it as occurring on the lakeward fringe of the bald cypress zone in southeastern Oklahoma. Davis (1937) also reports it on the lakeward side of flood-plain swamps of silver maple, willow and cypress in Reelfoot Lake in water about two feet deep. It invades open delta ponds at the mouth of the Mississippi River before the cypress swamps dominants (Lynch, 1940). In discussing the ecological niche of this grass, Penfound et al. (1938) state that "the cut grass is not only an ever present species in open cypress–gum swamps but forms a narrow zone along the borders of dense stands and is apparently a

good site indicator for this community". Although other species may occur in open stands of the cut grass, "this aggressive rank-growing plant exists in almost pure stands since no herbaceous growth, not even cattail (*Typha latifolia*), seems able to compete with it" (Steenis, 1950).

The cattail–bulrush–maiden cane (*Typha–Scirpus–Panicum*) marshes were described by Penfound et al. (1938) as the *Typha–Scirpus* associes. *Panicum hemitomon, Scirpus californicus, Typha angustifolia* and *T. latifolia* were listed as the predominant species. Kearney (1901) states that the *Typha–Sagittaria* association occurs in six to 12 inches of water in the Dismal Swamp, and gives *Typha latifolia* and *Sagittaria lancifolia* as the important dominants. Wells (1928) lists *Typha angustifolia, T. latifolia* and *Scirpus validus* as the dominants of the fresh water marsh (*Typha–Scirpus* associes). He states, however, that "over 450 species probably occur in this community in North Carolina if we include the plants of moist meadows, which should best find a place here". In fresh water ponds at the mouth of the Mississippi River, *Scirpus validus, Typha angustifolia, T. latifolia* and *Zizaniopsis miliacea* are listed as the dominant species (Lynch, 1940). The close relationship of the cattail–bulrush–maiden cane marshes to the everglades is emphasized by the fact that Davis (1946) lists *Sagittaria lancifolia, Pontederia cordata, Panicum hemitomon* and *Typha latifolia* as among the "most typical plants" of the saw-grass marshes. Of the dominants listed by Penfound et al. (1938), *Panicum hemitomon* is a strictly fresh-water species, but *Scirpus californicus, Typha latifolia* and *Typha angustifolia* are tolerant of considerable salt and may be found in slightly brackish marsh areas.

The saw-grass (*Mariscus jamaicensis*) marshes are most extensive in Florida, but occur in most of the southern coastal states. Saw-grass is the predominant plant of the Everglades. The saw-grass community is also present along the Pasqutank River in the Dismal Swamp area, but the individual plants do not grow as large as they do in the Everglades (Kearney, 1901). In southeastern Louisiana "the nearly fresh (faintly brackish) marsh is characterized by a nearly pure stand of saw-grass". "Associated with the saw-grass, especially in deeper water, are broadleaf cattail, the narrowleaf cattail, and giant bulrush" (Penfound et al., 1938). It should be noted that the saw-grass is always associated with faintly

brackish conditions (0.1 to 0.4 per cent of salt) in southeastern Louisiana.

SHALLOW FRESH-WATER MARSHES

The shallow marshes are grass–sedge–rush communities which are developed on acid soils, especially on the lower coastal plain. They have been referred to as rush marshes or wet prairies (Davis, 1946), grass–sedge bogs (Garren, 1943), wet meadows (Hotchkiss et al., 1947), low marshes (Kearney, 1901), pitcher-plant lands (Pessin, 1933), grass–sedge bogs (Wells, 1942) and moist pine barrens or savannahs (Wright et al., 1932). Undoubtedly there are several communities represented here. In general, the communities include several species of *Panicum* and *Rynchospora* as dominants with species of *Eriocaulon, Rhexia, Sarracenia* and *Sphagnum* as common associates. *Spartina bakeri* is a dominant in Florida (Davis, 1946); species of *Carex* are important in Maryland (Hotchkiss et al., 1947); and species of *Carex, Eleocharis* and *Juncus* are common in the low marsh (*Rynchospora–Eleocharis* association) of Kearney (1901). Pessin (1933) lists *Campulosus aromaticus,* and Wells (1942) includes *Aristida stricta* and *Campulosus aromaticus* as important dominants.

Shallow marshes originate by cutting and burning of the shrub swamps or of the red bay–sweet bay swamps (Wells, 1942). In Louisiana they arise directly upon cutting of the longleaf–slash pine type (Garren, 1943; Penfound et al., 1937; Pessin, 1933). Since shallow marshes "typically exhibit a mineral soil" (Wells, 1942), it is felt that they are formed mainly through cutting of the low pine forests and are maintained by recurring periodic fires.

Usually the shallow marshes include several species of *Sphagnum,* many of which are present in the sphagnum bogs of the northern states. Rigg (1951) queried many investigators as to whether any true sphagnum bogs occur in the southern States. The consensus seems to be that there are no southern sphagnum bogs which are comparable to those in the northern North America. According to H. L. Blomquist, "There are no extensive sphagnum bogs in North Carolina. However, there are numerous boggy areas in which some *Sphagnum* grows . . .". A. J. Sharp says that "there are no large bogs in Tennessee and all the small ones are shallow". There seems to be agreement that *Sphagnum* does

not encroach on other plant communities or form sedge–*Sphagnum* mats over water except in West Virginia, which is not considered a southern State in this report. It seems to be true also that " the surface layer of growing and partly dead *Sphagnum* probably adds very little if anything to the accumulation of peat, because of the high rate of oxidation of debris during most of the year, especially in dry seasons " (Rigg, 1951).

The shallow marsh is similar to the evergreen shrub swamp in many respects. Both are characterized by inundation in the early portion and desiccation in the latter part of the growing season. Both occur in soils which are highly acid and of low calcium content, factors which are carrelated with the high carbonaceous state of the plants (Albrecht, 1940). Because of the high fiber content of the plants, they burn readily, the shrub swamps burning every few years and the shallow marshes commonly burning over every year (Wells, 1942). Both communities, therefore, are fire serclimaxes which have been greatly enlarged by the more frequent fires of the white man. The herbaceous community has increased even more rapidly than the shrub associes, since deliberate annual burning is a common phenomenon in the lower coastal plain (Wells, 1942).

SALT MARSHES

The salt cane (*Spartina alterniflora*) marsh occurs throughout all the Atlantic and Gulf coastal States in saline areas near the sea. In Louisiana it often occurs in pure stand or with salt grass (*Distichlis spicata*) and black rush (*Juncus Roemerianus*) as less abundant associates. Similar salt cane communities have been described on Ocracoke Island (Kearney, 1900), on islands off the coasts of Mississippi and Louisiana (Lloyd et al., 1901) and for the Dismal Swamp (Kearney, 1901). For the salt-cane marsh (xeric salt marsh) in North Carolina, Wells (1928) lists five socies and indicates the probable successional relations. Along the North Carolina coast " the individual plants reach their best development about halfway between low and high-tide levels " (Reed, 1947). When fresh-water ponds near the mouth of the Mississippi River are cut off from fresh water, they are invaded by *Spartina alterniflora*. This suggests that the salt cane has a wide toleration of salinity (0.55 to 4.97 per cent, according to Penfound et al., 1938).

The *Spartina–Distichlis–Juncus* associes is a brackish marsh, famous for the production of muskrats. The dominants are couch grass (*Spartina patens*), salt grass (*Distichlis spicata*) and black rush (*Juncus Roemerianus*). This marsh " may be represented by pure stands of couch grass in slightly brackish areas or by pure stands of black rush in sandy areas, but there is usually an admixture of one or both of these species with the salt grass " (Penfound et al., 1938). This community on Ocracoke Island was designated as the *Juncus Roemerianus* association by Kearney (1900). It usually occurs in almost pure stands but includes *Distichlis spicata, Aster subulatus* and *Aster tenuifolius* as characteristic species. Lloyd et al. (1901) described a muck marsh association of *Spartina patens* and a sand–muck marsh association of *Juncus Roemerianus.* Lynch (1941) found that the composition of this marsh changed radically with fire, and that the deeper the fire, the greater the destruction of the marsh dominants.

The coastal marsh (*Spartina–Sporobolus* associes) occurs in southwestern Louisiana and along the Texas coast. Inland it grades imperceptibly into the coastal prairie. " The principal dominant over the area is *Spartina spartinae,* though *Sporobolus virginicus* shares dominance to a lesser extent " (Tharp, 1926). From the list of companion species given by Tharp it is obvious that the coastal marsh is one which is inundated only periodically. According to the classification used herein, it might be classed as a zonal or transitional community.

The salt grass (*Distichlis spicata*) consocies is a zonal salt water marsh community. In North Carolina, where the *Spartina alterniflora* consocies occurs, the next shoreward community is either the *Distichlis spicata* consocies or the *Spartina patens* marsh (Reed, 1947). In Louisiana the most common associates are sea ox-eye (*Borrichia frutescens*) and (southward) black mangrove (*Avicennia nitida*). Although Reed (1947) found that the salt grass " grew best in water of comparatively low salinity ", it has been observed mainly in areas of moderate to high salinity of soil water (0.47 to 4.97 per cent) in Louisiana (Penfound et al., 1938).

The reed–cane zone (*Phragmites–Spartina* associes) is a zonal (transitional) community which occurs just above the salt grass consocies and immediately below the buckbrush–marsh elder swamp. The *Phragmites–Spartina* associes is conspicuous through-

out the salt marsh area, since it occurs on the stream ridges and is composed of large grasses eight to 16 feet tall. The reed, *Phragmites Phragmites,* and the quill cane, *Spartina cynosuroides,* are the major dominants, although switch grass, *Panicum virgatum,* may be important locally. In general, the community occurs where the average water table is about four inches below the soil surface (Penfound et al., 1938). In relatively fresh-water areas, however, the dominants, especially quill cane, occur where the water table is very close to the soil surface. In such cases the reed–cane zone is quite extensive and approximates a true marsh.

MINOR MARSH TYPES

In the fresh-water sere there are several minor marsh or marsh-like communities not heretofore mentioned. The so-called "flag marshes" described by Davis (1943) consist mainly of *Pontederia cordata, Sagittaria lancifolia* and *Thalia dealbata.* These marshes are common in shallow ponds and sloughs, mostly in sandy areas in South Florida. The "prairies" of Wright et al. (1932) are similar but more diversified in plant composition. These pseudo-marshes, largely devoid of grasses, sedges and rushes, are common also in southern Louisiana as medial stages in the development of water hyacinth mats into marshes.

A so-called marsh of *Sphagnum* spp. and *Woodwardia virginiana* occupies open parts of the Dismal Swamp (Kearney, 1901). The same community occurs in very shallow water in the Okefinokee Swamp (Wright et al., 1932). Along the edges of the swamp forest of the Dismal Swamp, extensive cutover areas are occupied by the *Scirpus–Erianthus* association in which *Scirpus cyperinus* and *Erianthus saccharoides* are the major dominants (Kearney, 1901). Another community of the openings of swamp forests is the bur-reed marsh. This marsh, composed mostly of *Sparganium americanum,* may be seen at the Blue Girth Swamp, near Selma, Alabama (Hall et al., 1943).

Several minor marsh and transitional communities occur also in saline areas. Successional stages of *Scirpus americanus,* occur in fresh and slightly brackish areas throughout the South. On freshly deposited silt at the mouth of the Mississippi River, "*Scirpus americanus* is the initial colonizer, invading by means of seeds, and immediately assumes temporary dominance" (Lynch, 1940). Consocies of *Scirpus Olneyi* occur throughout the brackish marsh as

disclimaxes caused by fire or by the concentrated feeding of muskrats (Penfound et al., 1938). Tidal flat communities of *Salicornia Bigelovii* and *S. perennis* are common on mud flats and sandy places (Uphof, 1941). This community is designated as the *Batis–Salicornia–Spartina–Dondia* associes by Davis (1943) who states that "*Salicornia* and *Batis* are found in the most salty situations that support plant life". A somewhat similar community (beach consocies) occurs at the mouth of the Brazos River, Texas (Tharp, 1926). In addition to *Batis, Salicornia* and *Sesuvium,* the latter community includes *Monanthochloe littoralis* which is still more prominent in the Florida Keys (Davis, 1943).

PLANT SUCCESSION

"A prevalent concept in aquatic ecology is that water depth is primarily in control of the communities, with these zoned in a simple sequence from the shore outward" (Wells, 1942). Weaver et al. (1938) list the stages as follows: submerged → floating → reed-swamp → sedge-meadow → woodland (*Alnus, Salix,* etc.). Approximately the same sequence occurs at Reelfoot lake; submerged aquatics → transition zone (*Nelumbo*) → the marshes (*Zizaniopsis*) → willow forest (Davis, 1937). A similar sequence of stages occurs in nearly fresh areas in the marshlands of southeastern Louisiana: submerged → floating (*Castalia*) → marshes (*Mariscus*) → willow-border (Penfound et al., 1938).

The submerged stage is usually present in the hydrosere but less commonly in the halosere. Among the submerged species, the stoneworts (Characeae) are usually thought of as temporary species which occur in the deepest water. However, Wood (1950) found that they may be present for 50 or more years in a given habitat and that "they may occur above, amid, and below the zone of attached aquatic plants". Important submerged angiosperms in southern United States include *Ceratophyllum demersum, Cabomba caroliniana, Myriophyllum pinnatum, Naias guadalupensis, Philotria canadensis, Potamogeton pusillus, Vallisneria spiralis* and *Zannichellia palustris. Cymodocea manatorum, Ruppia maritima* and *Thalassia testudinum* are predominant in salt water habitats. Field observations suggest that there is zonation among the above submerged aquatic angiosperms, but insufficient data are at hand to attempt any arrangement with respect to water depth.

Field experience indicates that there is zonation also among the

floating-leaved aquatics. The larger and possibly more important genera (*Brasenia, Castalia, Nelumbo, Nymphaea*) occur in relatively deep water (as much as eight feet), whereas species of the smaller genera (*Alisma, Bramia, Heteranthera, Hydrocotyle, Veronica*) occur in shallow water (down to two feet). Excellent zonation is evident among the emergent aquatic plants. Among those which tolerate relatively deep water are *Dianthera americana* (to six feet deep) and *Zizaniopsis miliacea* (to four feet deep). These emergent species may occur in water similar in depth to that of many of the floating-leaved and submerged species. In view of the paucity of our knowledge on the relation of plants to water depth it is suggested that an investigation on the tolerance of all aquatic plants to water depth might be a rewarding one and contribute much to our knowledge of plant succession in the hydrosere.

Under certain circumstances, submerged and floating-leaved stages are lacking in the hydrosere, and marsh dominants may become established in relatively deep water. Along sluggish streams in Louisiana, *Zizaniopsis miliacea* becomes established on the inside of meanders, although no submerged or floating stages are present. A similar situation is found at Lake Roebuck (an ox-bow lake) in southeastern Oklahoma. The submerged and floating-leaved stages are absent also from many of the reservoirs of the Tennessee Valley Authority where *Dianthera americana* invades water as much as six feet in depth.

Submerged, floating-leaved and sedge-meadow stages are usually absent wherever perennial floating mats can develop. In the southern coastal States, water hyacinth "plays a predominant role in the fresh water sere by providing a floating platform upon which numerous other plants become established" (Penfound et al., 1948). The alligator weed (*Achyranthes philoxeroides*), another mat-forming species, often ecizes early on the water hyacinth mat and is important in expediting the formation of flotant. Altogether, the above authors listed 63 species that occurred on the water hyacinth mat. If any submerged or floating-leaved species are present when the mat begins to develop they are rapidly shaded out. In about 25 years "the mat is transformed into a flotant (floating prairie) comprising one or more of the following species: beef-tongue, cattail, cut grass, giant bulrush, maiden cane, saw-

grass, and water fern" (Penfound et al., 1948). Such a flotant, formed directly on the floating platform of water hyacinth, is essentially a marsh.

Hunt (1943) describes a somewhat similar condition at Goose Creek Reservoir, South Carolina. In this case, water hyacinth is absent but "*Alternanthera philoxeroides* . . . together with *Jussiaea grandiflora* forms the warp and woof of the mat, the base upon which the cat-tails later start". The *Typha latifolia* zone varies from 25 to several hundred feet in width. Between this and the main body of the mat is a narrow shrub zone of *Salix nigra* and *Cerothamnus ceriferus*. The main body of the floating mat consists of *Rufacer rubrum* with occasional specimens of *Tamala pubescens* and *Taxodium distichum* usually growing on a thick base of *Sphagnum*. In the above report the submerged, floating-leaved and sedge-meadow stages are all lacking, and a swamp forest develops directly on the floating mat.

The common concept of aquatic plant succession is that the bottom is built up by inorganic and organic sediments until such time as the water shallows sufficiently to allow emergent aquatics and finally wetland and terrestrial species to become established. Penfound et al. (1948) reported three mats which were about two feet thick but with nearly seven feet of water between them and a few inches of the sludge on the bottom. From a series of observations in Louisiana and at Orange Lake, Florida, these authors concluded that flotant builds from the surface downward and not from the bottom upward. Support for this view is also given by Hunt (1943) who states that "Here and there portions of the mat have sunk too rapidly, with destruction of the woody plants. This sinking occurs during the winter, when some of the vegetation dies back". Apparently the entire floating mat sinks somewhat every winter but receives an increment at the top every summer until such time as it is thick enough to support trees or until its base comes to rest on the bottom.

The absence of submerged and floating-leaved stages is the rule in inland salt water habitats. In Louisiana a submerged stage of *Ruppia maritima* may be present, but the marsh (reed-swamp) dominants usually become established in shallow ponds without intervening submerged and floating stages. In brackish areas, ditches and ponds with silt or clay bottoms are usually invaded by

Spartina alterniflora. After organic matter is built up this species is replaced by dominants of the brackish marsh (*Spartina–Distichlis–Juncus* associes). In saline areas *Spartina alterniflora* invades shallow water directly and remains the major dominant unless the areas are aggraded by inorganic sediments. Since *Spartina alterniflora* favors aggradation by sand and silt, it promotes the establishment of communities of *Distichlis spicata* or *Spartina patens* (Reed, 1947).

Buell (1939) reports a case where all the herbaceous aquatic successional stages are absent. In Jerome Bay, North Carolina, "The principal pioneer is the pond cypress, *Taxodium ascendens* Brongn., which becomes established on the exposed lake bottom during the dry seasons when the water is low". "Once the cypresses are established their buttressed bases and knees become nuclei for islands of shrubs and trees". "In contrast with conditions prevailing in most northern bog lakes there is almost no herbaceous aquatic vegetation" (Buell, 1939). Another case where woody vegetation directly invades the open water is that of the red mangrove, *Rhizophora Mangle. Rhizophora* seedlings may become established on mineral soils (sands, marls, shell fragments) in the absence of herbaceous aquatics and produce a closed red mangrove swamp in 30 to 50 years (Davis, 1940).

The grass–sedge stage of succession was not encountered in the Mississippi alluvial plain. It is common, however, in the coastal plain and in prairie areas. The wet prairies in Florida (Davis, 1946) and the low marshes of Kearney (1901) are later natural successional stages than the true marshes. On the other hand, the grass–sedge bogs (savannahs) of Pessin (1933), Wells (1942) and Wright et al. (1932) are areas of wet cut-over pinelands which are kept in a subclimax stage by fire. Most of the grass–sedge stages in the southern States are apparently of this nature and are properly designated as fire subclimaxes.

In many cases the succession in a given pond does not progress beyond the grass–sedge or shrub stage. This is true in the Bellair sand region of northern Florida where "the areas between high and low water marks around the ponds which fluctuate several feet are treeless, with a characteristic vegetation of herbs and scattered shrubs . . ." (Harper, 1914). In the flatwoods of southern Florida there are many "approximately circular depressions, varying in

extent from one to many acres which may hold a foot or two of water in wet weather, and become entirely dry in spring". They frequently contain only scattered shrubs or nothing but herbs. The predominant species include one characteristic shrub, *Hypericum fasciculatum*, and the following herbs: *Centella repanda, Eleocharis cellulosa, Erigeron vernus, Juncus repens, Spartina Bakeri* (Harper, 1927).

Displacement of marshes (reed-swamps) by swamp forests is fairly common throughout the southern States. In the Indian Village Swamp, Louisiana, there were patches of two marsh types (*Zizaniopsis miliacea* and *Mariscus jamaicensis*) which were being invaded by dominants of the cypress–gum swamp. A graded series of swamp trees (large to small) occurred between the main body of the swamp and the marsh patches. Further confirmation of marsh → swamp succession was provided by the fact that partially decomposed marsh grasses were found from two to three feet below the swamp forest floor (Hall et al., 1939). One of the most interesting cases of marsh → swamp succession is that reported by Hunt (1943). In this case a cattail marsh is replaced by a swamp forest, although both communities are developed on a floating mat. Even in salt-water areas displacement of marshes by swamps is common. "The salt-marsh vegetation decreases southward because of increasing competition with the mangrove . . ." (Davis, 1940). *Spartina alterniflora* either exists as an understory in, or is displaced completely by *Rhizophora Mangle*, and the salt grass (*Distichlis spicata*) zone is partially or largely eliminated by *Avicennia nitida*.

HABITAT FACTORS

Although many investigators have studied southern swamps, very few have discussed the habitat factors which affect the distribution of swamps and marshes or that determine the successional stages leading to these community types. Wells (1942) states that water depth is important in the control of aquatic communities, but that texture of the substratum may be more important than water depth. For the marshland of Louisiana, Penfound et al. (1938) state that "Water level and salinity of the soil water appear to be the most important, although soil moisture may be influential locally or during unfavorable periods". For mangrove swamps

and associated communities, Davis (1940) included salinity of the surface water and soil solution, tides, water levels and soils as the major environmental factors. In Reed's (1947) summary of the work of investigations on the zonation of vegetation in salt marshes, the factors of aeration, subsidence, osmotic pressure of the soil solution, soil acidity and plant competition are added. A fairly complete list of habitat factors is given below in outline form.

FACTORS RELATED TO COMMUNITY DISTRIBUTION

Physical factors	*Biotic factors*
Water	Plant competition
Water content	Animal actions
Water table	Human activities
Fluctuation	Levee-building
Soil type	Canalizing
Aeration	Road-building
Nutrients	Cutting
Acidity	Burning
Salinity	Draining
Temperature	Grazing
Light	Farming
Molar agents	

Apparently the factors which affect the distribution of swamps and marshes are somewhat different from those which determine the successional stages leading up to these swamps and marshes. The three great groups of swamps and marshes are the circumneutral ones of large river floodplains, the peat-forming communities of the uplands (especially on the coastal plains), and the salt-water associes and consocies along the sea coasts. The most important factors separating the circumneutral from the peat-forming hydric communities are soil type and acidity. In the large river floodplains (e.g., Mississippi River floodplain) the soils are mainly silts and clays with a typical pH range of 6.5 to 7.5. The soils of the coastal plains are sandy and have a typical pH range of 4.5 to 6.5. Obviously the important factor that is responsible for the salt-water swamps and marshes is the degree of salinity. The salt-water communities of South Florida are divided into northern and southern subtypes, the latter being distinguished by tropical mangroves whose northward extension is limited by low winter air temperatures.

The major factors in the establishment of the various circumneutral swamps and marshes are water depth, fluctuation of water levels and salinity. Swamp and marsh communities are to be correlated with fluctuating and stable water tables, respectively.

" This is due to the fact that cypress and gum seeds will germinate only in the presence of gaseous oxygen and not in water " (Wells, 1942). Salinity is often a factor in the coastwise limitation of fresh-water swamps and marshes. " Evidence seems to indicate that the transition from 0.4 per cent to 0.6 per cent in the average salinity of the soil water is responsible for the elimination of the cypress–gum swamp . . . ". Fresh-water marshes are also replaced by faintly brackish marshes (*Mariscus* consocies) when the above salinity is reached (Penfound et al., 1938).

Most animals except man are relatively unimportant in modifying the composition of swamps and marshes. The beaver often destroys existing wetland and terrestrial vegetation by constructing dams. This operation also creates new bare areas for the invasion of aquatic plants. In the brackish marshes, muskrats often become so abundant in a given locality that they consume most or all of their food supply consisting mostly of rhizomes of grasses, sedges and rushes. This changes the area from a relatively firm peaty marsh into a soupy shallow pond which is then available for invasion of aquatic plants of earlier successional stages. At the mouth of the Mississippi River geese often change extensive stands of *Scirpus americanus* into a semi-fluid mud flat by eating the rhizomes of this species. Grazing is important only in the zonal marsh communities such as the coastal marsh, although cattle may wade out and feed in the true marshes.

Human activities have been exceedingly important in the destruction of some and the formation of other hydric communities. Building of levees along the Mississippi River, digging of canals, road-building, lumbering and drainage projects have changed the landscape greatly since the time of notable settlement in the South. During periods of extreme floods, crevasses in the levees have often resulted in raising the soil levels of swamps and marshes and in eradicating many of the component plants. Canalization often has resulted in freshening salt-water areas and bringing salt into fresh-water areas, and thus changing the composition of the vegetation therein. Lumbering has changed the composition of cypress–gum swamps tremendously, and with the aid of fire, has changed some swamps into marshes (Beaven et al., 1939). Drainage has changed thousands of acres of swamps and marshes into modified hydric communities where the drainage is imperfect or to terrestrial communities or farmland where the drainage is complete.

Burning is relatively unimportant in alluvial plains, but may be severe in both swamps and marshes during prolonged periods of low rainfall. According to Putnam (1951), "fall is the fire season, especially in those years where the usual summer drought extends into autumn and early winter". Fires in the bottomlands are usually surface fires which destroy young seedlings and saplings, scorch the bark of larger trees and under extreme conditions destroy saw-timber trees. In the fresh-water marshes fires cause little damage when surface water is present but may destroy all the marsh dominants as well as the component animal life during drought years when the water table is well below the marsh surface. In the coastal plain the red bay–sweet bay swamps and the pine pocosins do not require cutting or fire for their establishment, but one or both of these factors are prerequisite to the formation of white cedar swamps, evergreen shrub swamps and shallow marshes. Furthermore, recurrent fire is necessary for the maintenance of evergreen shrub swamps and shallow marshes.

The most important factors in accounting for the various salt marsh and zonal communities are water level, soil moisture and salinity of soil water. Water level and water content are responsible for zonation in a given salt-water area, and salinity is critical in limiting the distribution of the various brackish and saline marshes. Undoubtedly soil type is important, since the black rush forms pure stands on sandy soils. As pointed out earlier, temperature is the limiting factor in the northward distribution of the mangrove swamps. Light is exceedingly important in that the salt-marsh dominants may be shaded out by the red mangrove, the salt grass may be largely eliminated by the black mangrove, and the reed–cane components may be shaded out by the buckbrush–marsh elder swamp.

Of human activities, canalizing, burning and draining have been the most common modifying factors in salt-water areas. Radical changes in marsh composition have been wrought by bringing fresh water into salt-water marshes. Fires caused by lightning and spontaneous combustion occur in the brackish marshes of Louisiana (Viosca, 1931). Most fires, however, are set by trappers to prevent destructive fires, to facilitate trapping of muskrats, to accelerate spring growth and to promote the development of muskrat food plants. Cover burns (surface water present) change the composition somewhat by favoring production of the famed musk-

rat food plant, *Scirpus Olneyi.* Root burns (water table two to four inches below surface) kill off marsh dominants but allow emergent species to invade. Peat burns (water table one to four feet below surface), such as occurred in Louisiana in 1924, produce shallow lagoons in which only submerged species may become established. Drainage projects have also been initiated in brackish areas. Nearly all of these projects have failed, however, due to improper financing and high maintenance costs, and many areas have been reflooded. " Drained lands which have been reflooded not only become excellent wildlife areas, but they usually produce a greater variety and a greater quantity of wildlife than the original marsh or swamp which was drained " (Penfound et al., 1945).

FACTORS RELATED TO SUCCESSION

In plant succession in any hydric area the primary factors are aggradation of the level of the substratum by inorganic and organic sediments, with consequent lowering of the water table and subsequent increase in oxygen tension above that level. While these changes are going on, more mesic plant types are able to ecize in the modified portions of the area and plant competition is increased. " Competition always occurs where two or more plants make demands for light, nutrients, or water in excess of the supply. If there is enough of any one of these factors, such as water in a swamp, there is no competition for that factor " (Weaver et al., 1938). It is probable that nutrients are rarely a factor in the circumneutral floodplains and in the salt-water marshes. Hence, in the hydrosere or halosere, plants compete mainly for light, and light becomes the most important factor in reducing or eliminating the components of earlier successional stages.

The depth to which submerged plants grow is determined largely by the penetration of light, submerged attached angiosperms rarely being observed at depths of more than 20 feet. Since floating-leaved plants are rarely rooted at depths of more than eight feet, invasion of submerged zones by floating-leaved aquatics beyond this level is prevented. Although submerged plants are often found throughout much of the floating-leaved zone, the floating-leaved species usually eradicate most of the submerged plants by depriving them of sufficient light. In areas where the water is less than six feet deep, emergent (reed-swamp, marsh) species are able to ecize. " Obviously, the floating plants are at a great disadvantage as re-

gards light" (Weaver et al., 1938), and most or all of the floating species disappear. It has been pointed out earlier that the floating-mat species, such as alligator weed and water hyacinth, are able to form a continuous mat over submerged and floating-leaved plants and thus to eliminate them by shading. The sedge-meadow stage is largely absent throughout much of the South, but the species of the willow and cypress–gum swamp stage readily invade and shade out the marsh (reed-swamp) species.

Plant succession from open water to salt-water swamps and marshes has received some attention. In the formation of the red mangrove swamp, young seedlings of *Rhizophora Mangle* become established at or below mean low tide level. "In most instances, the youngest, smallest plants are in the deepest water, farthest away from the thicker stand of the body of the community" (Davis, 1940). In about 20 or 30 years the pioneer plants have increased in numbers and size so that "there are few or no openings in the foliage overhead". By this time most of the algae and herbaceous seed plants have been completely shaded out, and "only the abundant mangrove seedlings seem to thrive below the canopy" (Davis, 1940). The change, however, from *Rhizophora Mangle* → *Avicennia nitida* → *Conocarpus erecta* is accomplished mainly by aggradation of inorganic sediments. Succession in salt marshes is relatively simple, since the marsh components usually invade open ponds directly. In case submerged plants are present (*Ruppia maritima*), they are readily shaded out by the marsh components.

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